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DOES THE TEMPERATURE COEFFICIENT OF PERMEABILITY INDICATE THAT IT IS CHEMICAL IN NATURE?

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In a recent paper STILES and JORGENSEN[1] state that the absorption of hydrogen ions by tissues of the potato has the temperature coefficient of a chemical reaction (2.18–2.22). They apparently reach the conclusion that "the substance with which the acid reacts" is "presumably the plasma membrane or some part of it," and that the facts suggest the view "held by PAULI and SZÜCS, who regard the entrance of ions into the cell as due to the reversibility of such a reaction between ions and the plasma membrane." These statements, together with the title of their paper, "The effect of temperature on the permeability of plant cells to the hydrogen ion," indicate that they regard the temperature coefficient found by them as the temperature coefficient of permeability to hydrogen ions.

This view, if well founded, is of considerable interest, as it indicates that permeability is chemical[2] rather than physical in nature, since (unless vapor tension is a determining factor) no physical processes are apt to be involved in this case which have a temperature coefficient as high as 2.[3] In view of this the statements of STILES and JORGENSEN deserve careful examination.

It should be noted that the only criterion of permeability employed by them was absorption from a solution. Their method consisted in placing slices of potato in a solution of HCl and determining the loss of hydrogen ions from the solution by means of a hydrogen electrode.

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[1] Ann. Botany **29**:611. 1915.

[2] BROWN and WORLEY (Proc. Roy. Soc. London B. **85**:546. 1912) have shown that the temperature coefficient of absorption of water by seeds is 2, but it is not clear whether this applies to imbibition (or other processes) taking place inside the cells, or to the permeability of the protoplasm. If it is really the coefficient of permeability to water, it is by no means necessary to extend this conception to permeability to substances other than water.

[3] Cf. KANITZ, A., Temperatur und Lebensvorgänge. Berlin. 1915 (p. 165).

It may be observed in this connection that the absorption of dissolved substances by living cells has been employed extensively as a criterion of permeability. The amount of absorption is usually determined by analysis (of the solution or of the tissue) before and after the organism is placed in the solution. A more convenient method, which suffices in some cases, is to determine the conductivity of the solution. Nephelometry is also useful. Such methods may also be used to determine the excretion of substances by the organism.

The results obtained by these methods have been so largely misinterpreted that there is widespread confusion in regard to their significance. This confusion is due in part to uncritical technique and in part to overlooking some of the many variables involved in such experiments; but the principal difficulty lies in confusing permeability with absorption.

The nature of this difficulty is evident from the following illustration. Suppose a glass tube closed at one end by a membrane in contact with a solution to which it is freely permeable. The solution will pass through the membrane into the tube until equilibrium is established. If, however, we place in the tube something which precipitates the dissolved substance, more of the latter will diffuse in, and this will go on as long as the precipitation continues. It is not even necessary that the precipitation should occur, since the result can be obtained by causing the dissolved substance to unite with something within the tube so as to form a compound which cannot pass out through the membrane.[4] The dissolved substance will then continue to pass into the tube.

It is evident that the permeability of the membrane remains the same whether precipitation or other chemical action occurs or not. But while the permeability remains the same, the amount of adsorption will vary enormously.

This may be observed with the living cell. When a cell is placed in a dye which is precipitated within the cell (giving a visible precipitate), the absorption of the dye goes on as long as the precipitate continues to form, while in the case of a dye which is not precipitated (and which does not form a compound incapable of passing out), the absorption ceases as soon as the concentration within the cell equals that of the solution.

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[4] Cf. LOEB, J., Dynamics of living matter. 1906 (p. 72).

It is evident, therefore, that the temperature coefficient observed by STILES and JORGENSEN may be that of a chemical process[5] involving the union of hydrogen ions with some constituent of the cell other than the plasma membrane (or other surface), in which case it would have no bearing upon the problem of the nature of permeability.[6]

Some time ago the writer sought to throw some light on this problem in ascertaining the temperature coefficient of permeability by a method which is free from the objections just discussed. By this method[7] the electrical conductivity of living tissue was determined in such a way that it may be regarded as a measure of the permeability of the protoplasm.

In these experiments a series of disks of *Laminaria* were packed together (like a roll of coins) so as to form a solid cylinder about 2 inches in length. The electrical conductivity was then measured at various temperatures. The temperature coefficient obtained in in this way was 1.33. The tissue was subsequently killed, whereby the conductivity was increased to practically that of sea water. The temperature coefficient of the dead tissue proved to be 1.26, which is practically the same as that of sea water.

If most of the resistance were due to apparatus, cell walls (intercellular substance), and sea water, and these had low temperature coefficients (for example, 1.26), that part of the resistance which is due to living protoplasm might have a high temperature coefficient (for example, 2) without much raising the temperature coefficient of the total resistance. The resistance of the apparatus (and the sea water contained in it) was determined at each temperature and subtracted from the total (giving what is called the

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[5] Absorption may also play a part in this connection.

[6] Cf. Biochem. Zeitschr. **67**:272. 1914.

[7] Even if the hydrogen ion unites "with the plasma membrane or some part of it," the temperature coefficient of this process would not necessarily be the temperature coefficient of permeability.

net resistance), so that we need consider only the resistance of the protoplasm, of the cell walls imbibed with sea water, and of the capillary films of sea water between the disks.

When the net resistance is 1200 ohms, we find that on killing the tissue the resistance drops to about 100 ohms. Since this represents the resistance of the cell walls and of the sea water plus the resistance of the dead protoplasm, it is evident that the resistance of the cell walls and of the sea water together must be less than 100 ohms. So far as can be judged from microscopic measurements, the fraction of the cross-section of the conducting column occupied by the cell walls is less than half, and it is probable that when the net resistance is 1000 ohms, not more than 50 ohms are due to cell walls and to the sea water adhering to the tissues.[8]

It is evident, therefore, that if the resistance of the living protoplasm had a temperature coefficient of 2, the temperature coefficient of the total resistance would be only a little less than 2.

We may conclude, therefore, that the temperature coefficient of permeability is not far above 1.33. This indicates that permeability is not chemical in nature, although it is not absolute proof, as some chemical reactions have low temperature coefficients.

It would seem, therefore, that we cannot accept the idea that permeability is chemical in nature without much more conclusive evidence than we possess at present.

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[8] The problem is complicated by the arrangement of the protoplasmic masses.